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LONGITUDINAL DEVELOPMENT OF MACROINVERTEBRATE COMMUNITIES BELOW OLIGOTROPHIC LAKE OUTLETS

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ABSTRACT.—Benthic macroinvertebrates were collected at several sites downstream of three oligotrophic lake outfalls in July 1986. Total numbers, biomass, and species richness increased rapidly immediately downstream from the outlets, and then either stabilized or continued to increase downstream in parallel with benthic organic matter standing crops. Filter feeder densities showed an initial buildup and then decline downstream from the outlets. Variability in longitudinal patterns of other functional feeding groups among lake outlets was related to differences in food quantity and quality, and microhabitat.

An additional set of samples was collected at Pettit Lake outlet in August 1986. Species richness and total density peaked sooner under baseflow conditions in August than under spring runoff conditions in June. Distributions of all functional feeding groups, except filter feeders, also differed between the two periods, reflecting differences in the physical environment. We conclude that reduced lentic inputs of particulate organic matter seston and improved habitat suitability downstream are responsible for the progressive development of macroinvertebrate communities in oligotrophic lake outlets. These data imply the importance of the habitat template in the structuring of benthic communities.

Studies on the macroinvertebrate fauna in the outlet streams of meso- and eutrophic lakes have focused on the fate of lentic plankton or on longitudinal distribution of filter feeders in relation to progressively declining amounts of lake seston (Chandler 1937, Reif 1939, Cushing 1963, Maciolek and Tunzi 1968, Sheldon and Oswood 1977, Statzner 1978, Mackay and Waters 1986, Morin and Peters 1988). No comparable studies have been published for outlet streams of oligotrophic lakes. We hypothesized that streams draining oligotrophic mountain lakes would contain low levels of lake seston and that the invertebrate community would develop gradually as instream and adjacent riparian (allochthonous detritus) food sources developed. As a corollary, we expected that dense benthic filter feeder populations would not develop below the outlet or would dissipate

rapidly as the limited seston resource was rapidly utilized. Our ultimate aim was to use the oligotrophic lake outlet invertebrate community as an analogue to low-head hydroelectric diversions to determine the distance required for recovery to prediversion community conditions under the "worst case scenario" of total elimination of invertebrate drift.

METHODS

Description of Study Sites

Studies were conducted during 8–15 June 1986 on three lake outlet streams located within the Stanley Basin of central Idaho (115°00'W longitude, 44°07'N latitude). Specifically, the streams drained Yellowbelly Lake, Stanley Lake, and Pettit Lake. Both the Yellowbelly Lake outlet stream and the Pettit Lake outlet stream flow into Alturas Lake

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TABLE 1. Physical measurements characterizing the three lake outlet streams at each transect for the preliminary lake outlet study (June 1986).

TRANS*	DIST (m)	%	W (m)	D (m)	V (cm/s)	SUB (cm ³)	LRIP (m)	RRIP (m)
Yellowbelly Lake outlet			Temp = 13 C					
1	10	1	10	.70	49	275	7	7
2	20	1	13	.67	58	186	7	7
3	40	1	15	.44	54	77	8	7
4	80	1	12	.49	97	333	8	6
5	160	1	8	.55	87	657	8	13
6	400	1	20	.45	63	50	5	15
Stanley Lake outlet			Temp = 10.2 C					
1	30	1	12	.86	72	109	10	2
2	220	1	10	.50	122	1691	20	15
3	240	1	8	.51	135	337	8	20
4	250	1	15	.59	110	229	5	15
5	360	1	13	.62	96	497	35	8
6	600	1	NA	.54	115	83	25	40
7	1000	1	18	.50	109	167	16	20
Pettit Lake outlet			Temp = 14.8 C					
1	10	1	15	.65	50	8	15	25
2	20	1	15	.51	55	3	15	50
3	40	1	15	.56	77	385	15	10
4	80	1	10	.62	90	299	2	15
5	160	1	15	.46	93	323	15	10
6	400	2	12	.44	137	358	10	12
7	900	2	14	.47	109	281	2	6

*TRANS = transect, DIST = distance downstream from lake outlet, % = percent gradient, W = stream width, D = mean stream depth, V = mean stream velocity, SUB = mean size of dominant substrate, LRIP = width of riparian zone on left side of stream, RRIP = width of riparian zone on right side of stream. N = 5 for D, V, and SUB for each transect.

Creek, which flows into the Salmon River. Stanley Lake Creek flows into Valley Creek before entering the Salmon River near the town of Stanley, Idaho. The three outlet streams were chosen because of their relatively pristine conditions and the large size of the lakes. Motor boat usage occurs on Pettit and Stanley lakes during summer. In addition, Pettit Lake has summer homes situated on the east side. Yellowbelly Lake is accessible primarily by foot.

Seven transects were located on each stream at geometrically increasing points downstream from the lake outlet (Table 1), but only six transects were placed at Yellowbelly Lake outlet because of a fish migration barrier located further downstream. The barrier altered the natural geomorphology of the stream by backing up and slowing streamflow for 100 m. Below the barrier the stream gradient greatly increased, thus again interfering with placement of transect 7. A fish migration barrier was located at Stanley Lake about 200 m downstream of the lake outlet. This barrier backed up streamflow to within 70 m

of the lake. Here, transect 1 was placed 30 m downstream from the outlet and the remaining transects (2-7) starting 20 m below the barrier (about 220 m from the actual lake outlet, Table 1). Pettit Lake had a fish migration barrier located about 120 m downstream from the lake outlet. The barrier had no obvious effects on the natural streamflow; thus transect distances were left unmodified.

Physical measurements at each transect included percent gradient, stream width, mean stream depth, mean channel velocity, dominant substratum size, and width of the riparian zone on each side of the stream (Table 1). Temperature was recorded at midday for each stream. Generally, all three streams were similar in gradient (1-2%), stream width (10-15 m), stream depth (45-65 cm), mean stream velocity (70-120 cm/s), dominant substratum size (about 200 cm³), and riparian width (about 15 m) (Table 1). Yellowbelly Lake outlet stream had relatively slower channel velocities, probably due to the migration barrier below transect 6. The effect of the barrier also is evident in the reduction of the

TABLE 2. Comparison of physical measurements in the Pettit Lake outlet stream at each transect for both June (J) and August (A) 1986. Distances, gradients, and riparian zone widths remained the same on both dates (see Table 1).

TRANS*	W (m)		D (m)		V (cm/s)		SUB (cm ³)		Q (m ³ /s)	
	J	A	J	A	J	A	J	A	J	A
1	15	9	.65	.16	50	29	8	6	4.85	0.42
2	15	9	.51	.24	55	27	3	2	4.21	0.58
3	15	10	.56	.21	77	26	385	430	6.47	0.55
4	10	8	.62	.23	90	33	299	380	5.55	0.61
5	15	8	.46	.25	93	37	323	688	6.42	0.74
6	12	6	.14	.24	137	40	355	822	7.23	0.58
7	14	6	.47	.34	109	21	284	896	7.17	0.39

*TRANS = transect, W = stream width, D = mean stream depth, V = mean stream velocity, SUB = mean size of dominant substrate, Q = mean streamflow. N = 5 for each transect

dominant substrate size at transect 6 (Table 1). Stanley Lake outlet had a lower temperature than either Yellowbelly or Pettit Lake outlet streams (Table 1).

Pettit Lake outlet was chosen for a more extensive analysis in August 1986. The stream differed physically between the two study periods (Table 2). Mean stream width (by 4–5 m), mean stream depth (by 20–30 cm), mean channel velocity (by 30–100 cm/s), and mean streamflow (by 0.4–0.6 m³/s) were lower in August than in June (Table 2). The dominant substratum size increased in August (by 12%–219%) except at transects 1 and 2, where the substratum was predominantly coarse sand (Table 2). This change in dominant particle size could be attributed to the restricted area for sampling during low flows.

Collection Methods

Five macroinvertebrate samples were collected at each transect using a modified Hess net (210 μ m mesh). Five additional benthic samples were collected from each transect at Pettit Lake outlet in August 1986. The circular net was placed firmly on the stream bottom, and a railroad spike was used to disturb the substratum within the net to a depth of 10 cm. Large cobbles were scrubbed by hand and removed for inspection of invertebrates. The contents of the net were collected, preserved in 10% formalin, and returned to the laboratory for analysis.

In the laboratory the invertebrates were hand-picked, identified, and enumerated using a dissecting microscope (8X). Chironomids were identified to family. Macroinvertebrate biomass (dry mass) was determined by drying the samples at 60 C and weighing. The remaining debris from each sample was used

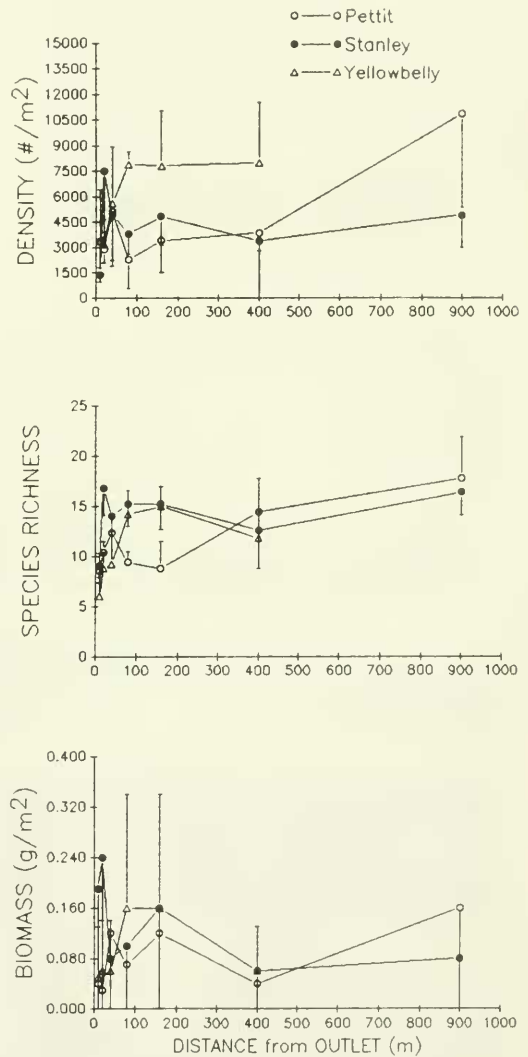


Fig. 1. Macroinvertebrate density, biomass, and species richness in three lake outlet streams in June 1986. Vertical bars indicate ± 1 standard deviation.

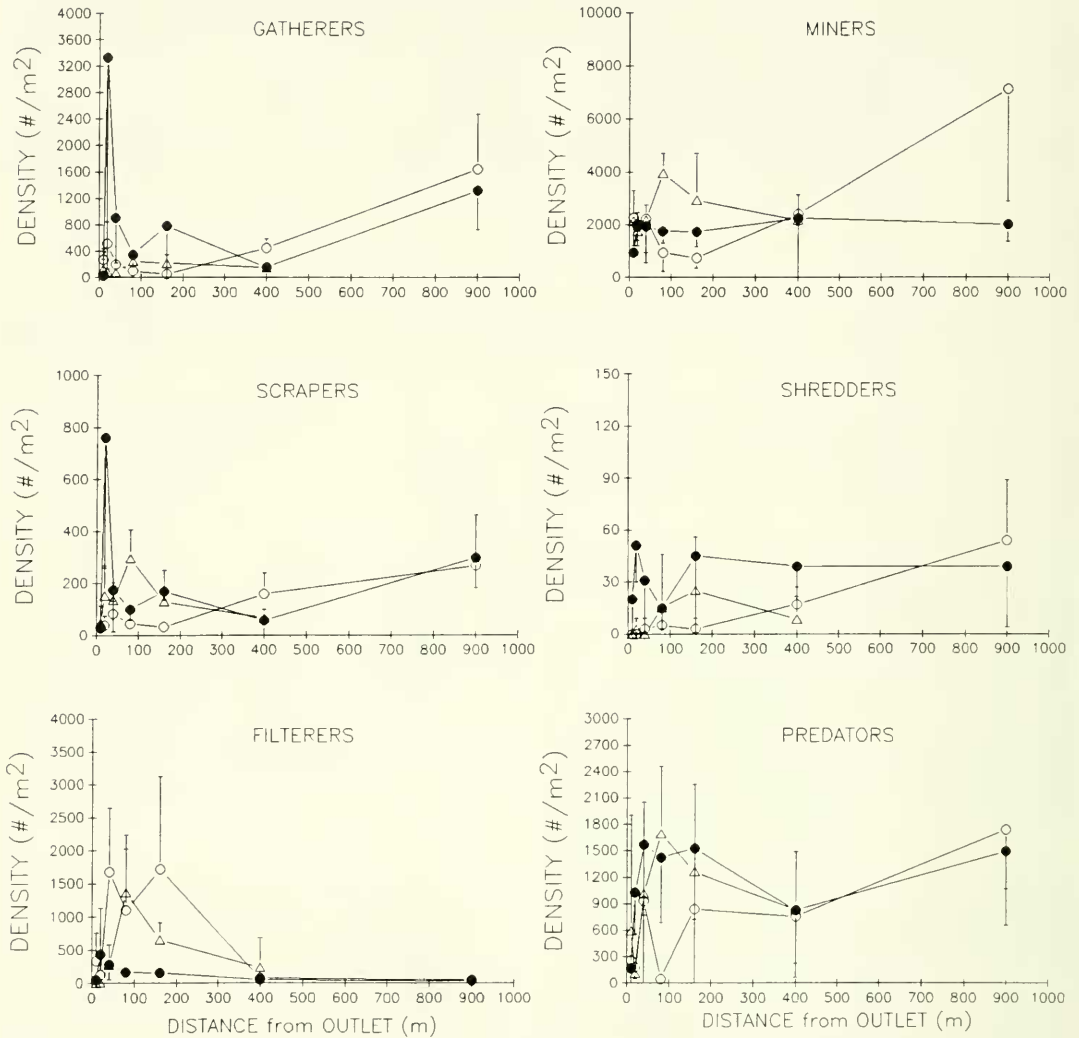


Fig. 2. Macroinvertebrate density by functional feeding group in three lake outlet streams in June 1986. Open circles = Pettit Lake, closed circles = Stanley Lake, and open triangles = Yellowbelly Lake. Bars represent ± 1 standard deviation.

to determine the amount of benthic organic matter (AFDM). The sample was dried at 60 C, weighed, ashed at 550 C, rehydrated, redried at 60 C, and reweighed.

RESULTS

Community Analysis

Macroinvertebrate density and biomass increased rapidly immediately below the outlets and then plateaued or, as in the case of Pettit and Stanley, decreased before stabilizing (Fig. 1). Total density and biomass at Stan-

ley and Yellowbelly Lake outlets plateaued within 40 m. Yellowbelly Lake outlet had densities twice those of Pettit and Stanley Lake outlets, although biomass was similar among sites. This was probably in response to greater food availability as reflected in differences in organic matter standing crops between the two locations (Fig. 1). Macroinvertebrate density in Pettit Lake outlet was lower than that in the two other outlets at 80 m, but showed a relatively rapid increase to levels exceeding those of Stanley Lake outlet at transect 7.

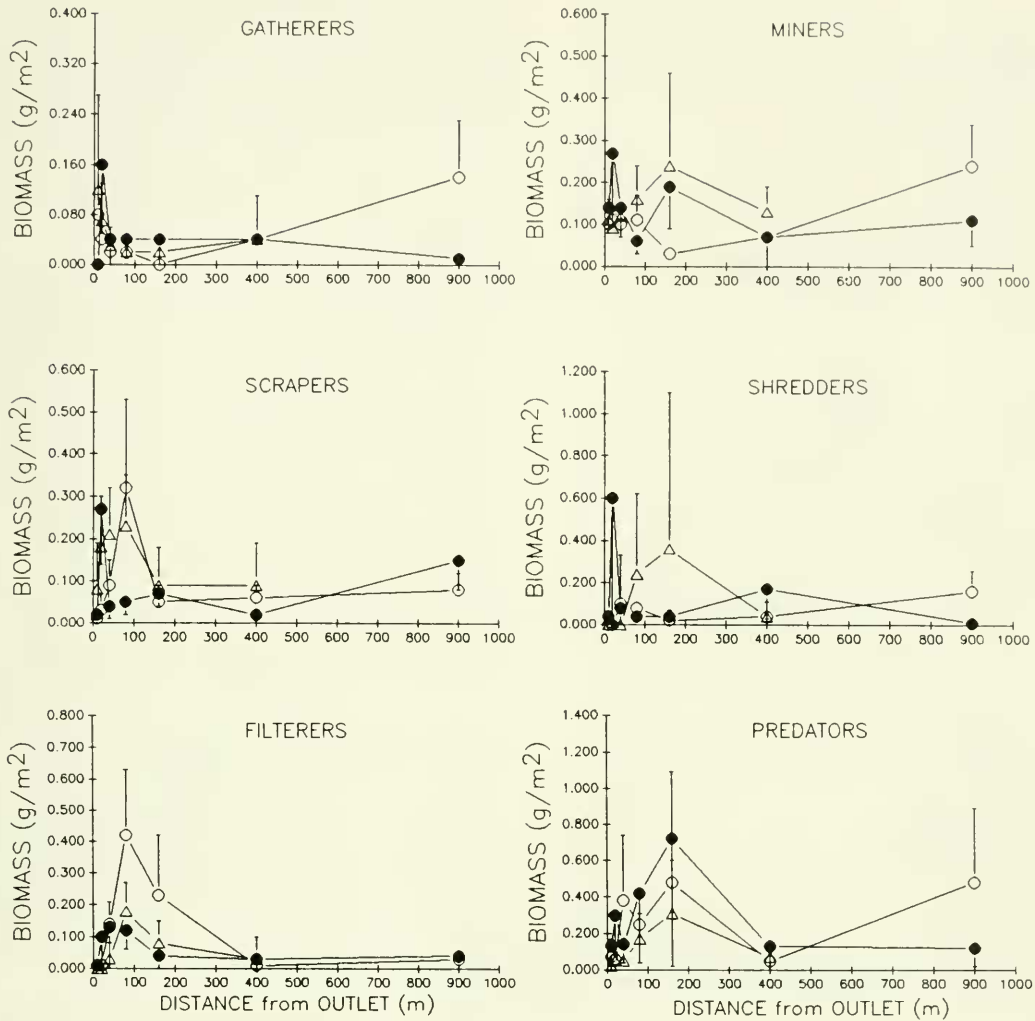


Fig. 3. Macroinvertebrate biomass by functional feeding group in three lake outlet streams in June 1986. Open circles = Pettit Lake, closed circles = Stanley Lake, and open triangles = Yellowbelly Lake. Bars represent ± 1 standard deviation.

Species richness increased immediately downstream from each lake outlet (Fig. 1). Pettit and Stanley Lake outlets showed slight declines in richness 20–80 m downstream, although there was a tendency, best seen at Pettit, to progressively add species with increasing distance from the lake.

Functional Feeding Group Analysis

STANLEY LAKE OUTLET.—The density and biomass of gatherers, scrapers, filterers, and predators each showed patterns comparable to that of total density and biomass (Figs. 2, 3). An exception was the extended high abun-

dance of predators at 40–160 m. Shredder density downstream of 160 m showed a resurgence to high values observed at 20 m rather than a maintenance of values comparable to those found at 80 m as occurred for total density. Miners did not show the marked peak at 20 m seen for total numbers and for other functional feeding groups. Miners, such as chironomids, have been found to be abundant in lentic sediments, which may explain their lack of response immediately below lake outlets.

PETTIT LAKE OUTLET.—Gatherer, scraper, and miner density and biomass all showed

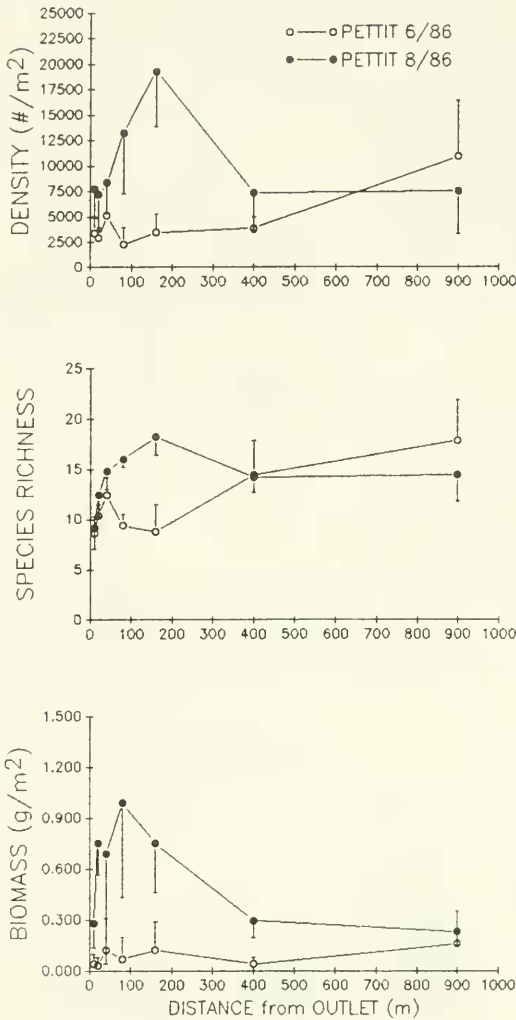


Fig. 4. Macroinvertebrate species richness, density, and biomass in Pettit Creek in June and August 1986. Bars represent ± 1 standard deviation.

patterns similar to those of total density and biomass. Filterer density and biomass peaked at 40 and 160 m (Figs. 2, 3). Predators showed an accentuated recovery in numbers at 160 m and continued high levels at 400 m in contrast to the pattern for total numbers. Predator biomass followed the pattern observed for filterer biomass (Fig. 3).

YELLOWBELLY LAKE OUTLET.—The density and biomass of gatherers, filterers, and predators showed patterns similar to those of total density and biomass. However, the predator biomass deviated from the general trend by decreasing downstream of the 80-m transect

(Figs. 2, 3). Filterer density and biomass peaked shortly below the outlet as was found at Pettit Lake outlet. The high filterer density and biomass were at a single location (80 m) rather than over an extended stretch (40–160 m) as at Pettit. Greater current velocity and substrate size may have facilitated colonization by filterers at 80 m at Yellowbelly Lake outlet (Table 1).

In general, the density and biomass of shredders followed the pattern seen for benthic organic matter at all three lakes. This was the “expected” pattern for all functional groups, based on the assumption of a lake outlet stream gradually accruing food downstream from allochthonous sources. Deviations from this pattern, especially by filter feeders, suggest “contamination” of the water by lake plankton. This was least evident at Stanley Lake outlet and most pronounced at Pettit Lake outlet. However, even at Pettit Lake outlet filter feeder populations declined rapidly within 160–400 m, indicating depletion of this material (Figs. 2, 3). Scraper density and biomass suggest that, for the most part, autochthonous sources of food were low, as would be expected for the headwater streams we were attempting to simulate. Yellowbelly Lake outlet at the 20-m transect is a notable exception. Although there were some minor deviations, data for density and biomass of functional feeding groups showed similar patterns (Figs. 2, 3).

Seasonal Study of Pettit Lake Outlet

Longitudinal patterns of total density, biomass, and species richness were somewhat different in August from those found in June (Fig. 4). Animal density, biomass, and species richness peaked sooner in August than in June and were not significantly different downstream of the 400 m transect. Total density and biomass increased downstream to 160 m, declined markedly for the next 240 m, and then stabilized in August (Fig. 3). The peak in abundance 40–200 m downstream of the lake outlets in August suggests greater production occurring at this time of year, possibly due to increases in stream temperature, solar radiation, and lentic inputs.

Longitudinal distributions of all functional feeding groups except filterers and scrapers differed in August from those in June (Figs. 5, 6). Filterer density and biomass peaked early

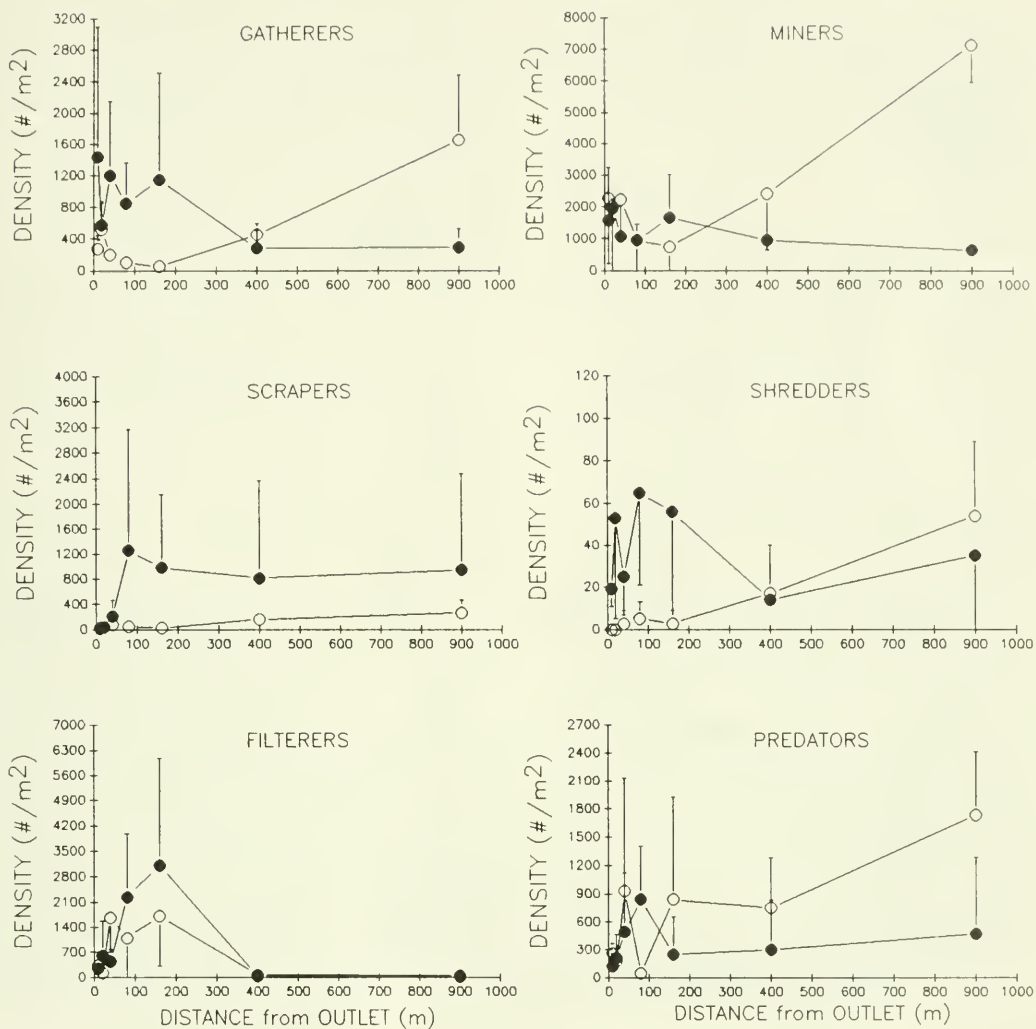


Fig. 5. Macroinvertebrate density by functional feeding group in Pettit Lake outlet in June and August 1986. Open circles = June, closed circles = August. Bars represent ± 1 standard deviation.

and then virtually disappeared from the community downstream for both sampling dates. Gatherers, miners, and shredders increased in abundance (density and biomass) downstream of the outlet in June, whereas gatherers, miners, and shredders had high densities through 160 m and then decreased to low values at 400 and 900 m in August. Gatherer, miner, and shredder biomass was similar among transects in August. Scrapers peaked in biomass at 80 m in June but displayed similar biomass values among transects in August (Fig. 6). The main difference in predator abundance between the two dates was the

reduced peak at 40 m and the decrease at 80 m in June that was absent in August (Figs. 5, 6).

DISCUSSION

The results support our hypothesis of a gradually developing stream community (greater numbers/m² and taxonomic complexity) with progressive distance downstream of a lake outlet. The distance required for the development of full community potential (i.e., the recovery distance following complete interception of incoming drift) could not be determined precisely and seems to vary

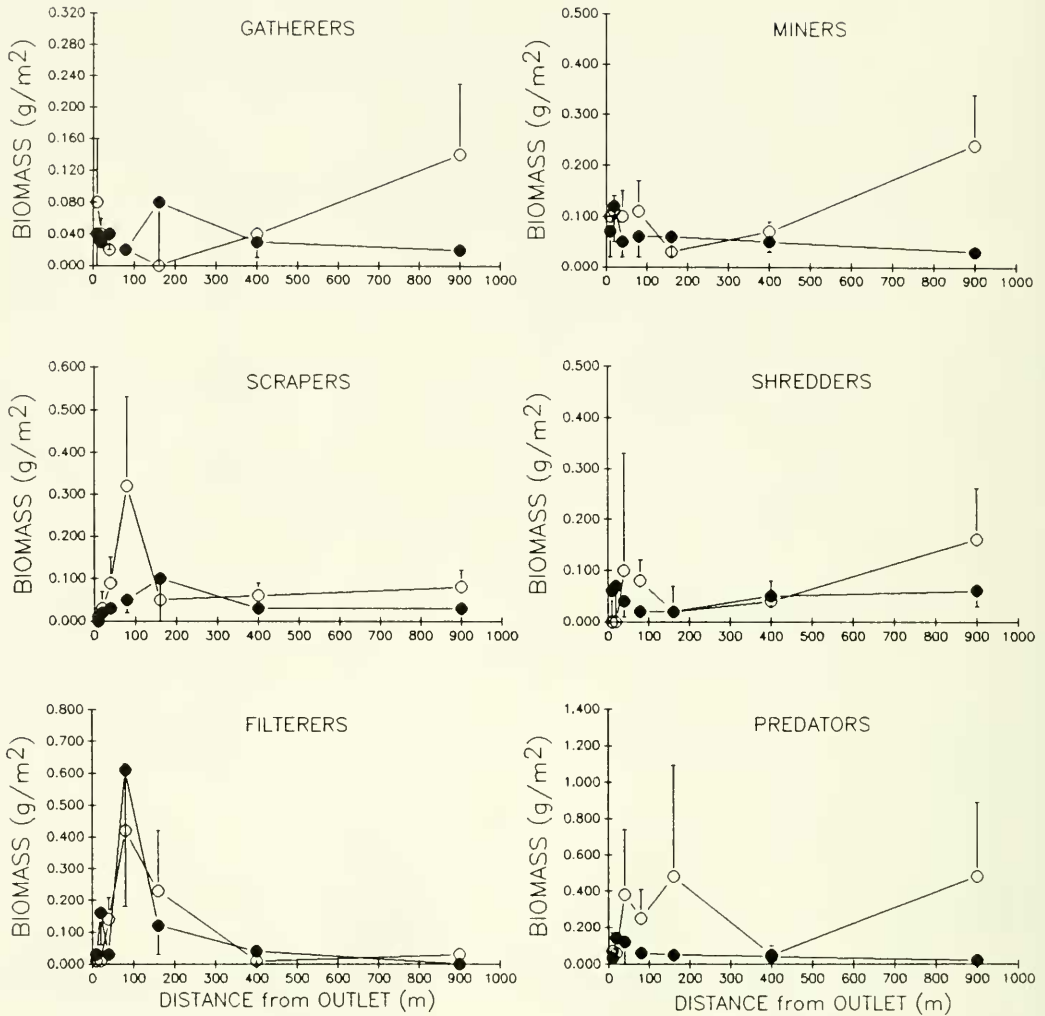


Fig. 6. Macroinvertebrate biomass by functional feeding group in Pettit Lake outlet in June and August 1986. Open circles = June, closed circles = August. Bars represent ± 1 standard deviation.

widely depending on the particular stream and time of year. In June, during a period of relatively high discharge, "recovery," measured in terms of species richness and total density, ranged from 20 m at Stanley Lake to over 900 m at Pettit Lake. During near base flow conditions in August, community development in Pettit Lake seemed to be much more rapid than in June, peaking somewhere between 160 and 400 m. These data suggest that community development is impeded under conditions of high flow. Additional measurements should be made in several outlet streams having unaltered flows and channels so that the full distances required for recovery

during each season and the factors responsible for the different rates of community development among streams can be established.

Our results also show a restricted distribution by filter feeders. The decline from peak numbers below the outlet was more rapid than reported by Sheldon and Oswood (1977), thus supporting our prediction that oligotrophic lakes will show more limited supplies of seston and consequently a more restricted distribution of filter feeders in their outlet streams than meso- or eutrophic lakes. In addition, we found that filter feeder abundances increased from low numbers immediately below the outlet to peak numbers some

distance (40–80 m) downstream. This differs from the progressive downstream decrease in filter feeder abundance modeled by Sheldon and Oswood (1977) and may have been overlooked by them because they sampled no closer than 25 m below the lake outlet. A parabolic relationship of filterer density with distance rather than a negative linear regression may be due to suboptimal environmental (e.g., velocity) or biotic conditions near the outlet. Current velocities in Pettit Creek were less near the outlet (26–29 cm/s) than further downstream (33–40 cm/s) and may not have met the needs of filterers for feeding or respiration. Further, changes in substratum characteristics occurred within 40 m of the lake outlet (Table 1). Mackay and Waters (1986) suggest that changes in filterer abundances between the impoundments they studied may be due to a greater abundance of attachment sites.

Our data contribute a spatial dimension to the recolonization of stream benthos by macroinvertebrates. These data suggest the importance of the habitat templet in the structuring of benthic communities. This implies faster recovery or community development in streams below lake outlets in which adequate structural habitat is present. These data suggest that low-head hydro installations can impact macroinvertebrate communities by reducing the structural attributes of the habitat templet.

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